Effects of Glyphosate on Photosynthetic Characteristics of the Invasive Plant Solidago canadensis and the Associated Plant Imperata cylindrica (Postprint)

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Abstract

The invasive plant Solidago canadensis has caused significant damage in many regions. Currently, chemical control methods are commonly employed for its management, but herbicides used to control invasive plants inevitably affect the growth of native plants. To investigate the effects of glyphosate on the photosynthetic characteristics of invasive and native plants, this study used Solidago canadensis and its associated species Imperata cylindrica as research subjects. A pot-controlled experiment was conducted to examine the growth characteristics and light response processes of monocultured and mixed-cultured S. canadensis and I. cylindrica under different concentrations of glyphosate treatment for 21 days. The results showed that: 1) Glyphosate significantly inhibited the growth of both plants. With increasing treatment concentration, the plant height increment of S. canadensis continuously decreased, while its leaf withering rate continuously increased; the tiller mortality rate and leaf withering rate of I. cylindrica continuously increased. I. cylindrica was more sensitive to glyphosate. At a concentration of 0.6 mL/L, I. cylindrica exhibited chlorosis first. At 1.2 mL/L, its tiller mortality rate and leaf withering rate both exceeded 50%. At 1.8 mL/L, the leaf withering rate of S. canadensis exceeded 50%. After herbicide application, compared with monoculture, mixed-cultured S. canadensis showed slightly faster plant height growth and slightly lower leaf withering rate, while mixed-cultured I. cylindrica had lower tiller mortality rate and leaf withering rate. However, the differences between monoculture and mixed culture were not significant. Interspecific relationships significantly affected the tiller number of I. cylindrica. 2) With increasing treatment concentration, the leaf net photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr) of both S. canadensis and I. cylindrica continuously decreased, with I. cylindrica decreasing more rapidly. The changes in intercellular CO2 concentration (Ci) differed between the two species. As concentration increased, Ci in monocultured S. canadensis first decreased and then increased, whereas Ci in mixed-cultured S. canadensis continuously decreased. Ci in both monocultured and mixed-cultured I. cylindrica increased. 3) Glyphosate significantly affected the maximum net photosynthetic rate (Pnmax), light saturation point (LSP), and light compensation point (LCP) of both S. canadensis and I. cylindrica. Its effects on dark respiration rate (Rd) of both species were not significant, and its effects on apparent quantum yield (AQY) of S. canadensis were also not significant, but it significantly affected AQY of I. cylindrica. Planting pattern significantly affected Pnmax and LSP of both species, as well as Rd and AQY of I. cylindrica. At 0.6 mL/L glyphosate, the effect on Pnmax of mixed-cultured S. canadensis and I. cylindrica was greater than that on monocultured plants. As treatment concentration increased, the effects on Pnmax of both plant species under different planting patterns tended to converge. Compared with the native species I. cylindrica, the invasive plant S. canadensis had higher photosynthetic and growth rates. Glyphosate significantly reduced the growth and photosynthesis of both species, with I. cylindrica being more sensitive to glyphosate treatment.

Full Text

Preamble

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Effects of Glyphosate on Photosynthetic Characteristics of Invasive Plant *Solidago canadensis* and Associated Plant *Imperata cylindrica*

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Abstract

Solidago canadensis, a serious invasive plant, causes considerable economic damage worldwide. Chemical control is widely used to manage invasive species, but herbicide application may negatively affect native plant growth. This study investigated differential photosynthetic responses to glyphosate treatment in invasive *S. canadensis* and native *Imperata cylindrica* using a pot experiment with monoculture and mixed planting patterns over 21 days under four glyphosate concentrations (0, 0.6, 1.2, and 1.8 mL/L). Key findings include: (1) Glyphosate significantly inhibited growth in both species ($P < 0.05$). Cumulative height growth and green leaf number in *S. canadensis* decreased with increasing concentration, while tiller mortality and leaf withering rate in *I. cylindrica* increased. *Imperata cylindrica* showed greater sensitivity, turning yellow at 0.6 mL/L, with withering rates exceeding 50% at 1.2 mL/L, whereas *S. canadensis* leaves only surpassed 50% withering at 1.8 mL/L. Mixed-culture *S. canadensis* showed slightly better growth (higher height increment, lower leaf withering) compared to monoculture, while mixed-culture *I. cylindrica* exhibited lower tiller mortality and leaf withering rates. (2) Glyphosate significantly reduced net photosynthetic rate (Pn) in both species ($P < 0.05$). Intercellular CO_2 concentration (Ci) responses differed: monoculture *S. canadensis* Ci first decreased then increased, while mixed-culture *S. canadensis* Ci continuously declined; both monoculture and mixed-culture *I. cylindrica* Ci increased with concentration. Stomatal conductance (Gs) and transpiration rate (Tr) decreased with increasing concentration. (3) Maximum net photosynthetic rate (Pmax) and light saturation point (LSP) declined while light compensation point (LCP) increased with glyphosate concentration. Dark respiration rate (Rd) and apparent quantum yield (AQY) of *S. canadensis* were unaffected, but AQY of *I. cylindrica* was significantly impacted. Planting pattern significantly affected Pn, Rd, and AQY of *I. cylindrica* and Pn of *S. canadensis*. The 0.6 mL/L concentration had greater effects on mixed-culture plants than monoculture plants. Compared to native *I. cylindrica*, the invasive *S. canadensis* had higher photosynthetic and growth rates but showed greater tolerance to glyphosate.

Keywords: herbicide; *Solidago canadensis*; *Imperata cylindrica*; growth; photosynthesis

Introduction

In the context of accelerating global change, biological invasions by alien plants have attracted increasing attention due to their threats to ecosystem structure, function, and biodiversity, causing enormous economic losses in invaded regions [1-3]. Chemical control remains a primary management tool, with glyphosate being one of the most widely used herbicides globally due to its high efficiency and low toxicity [4-6]. Glyphosate inhibits the shikimic acid pathway, blocking protein synthesis and chlorophyll formation, and disrupts photosynthetic processes including photophosphorylation, leading to physiological dysfunction [6-9]. However, during invasive species control, herbicides inevitably affect native plants either through direct contact or indirect soil-mediated effects [10-13].

Photosynthesis is fundamental to plant metabolism. Invasive species often exhibit higher net photosynthetic and relative growth rates compared to native species [14-16], with clonal integration further enhancing their resource acquisition efficiency in heterogeneous environments [17-18]. While glyphosate effectively suppresses many invasive species [5,7,19-20], its sublethal concentrations can negatively impact native crop growth and photosynthesis [21-24]. Few studies have compared herbicide effects on co-occurring invasive and native plants.

Solidago canadensis (Asteraceae), a perennial herb, severely impacts coastal ecosystems in eastern China, invading diverse habitats including native *Imperata cylindrica* communities [25-28]. This study examines glyphosate effects on growth and photosynthetic characteristics of both species to assess differential responses and provide data supporting rational herbicide use.

1. Study Area

The study was conducted in the ecological conservation zone of Hangzhou Bay National Wetland Park in Ningbo, Zhejiang (121°08 43 E, 30°18 40 N). The region has a mean annual temperature of 16.0°C, with monthly averages ranging from 3.8°C (January) to 28.2°C (July). Annual precipitation is 1344.7 mm, annual sunshine duration approximately 2038.4 hours, soil salinity 1‰–5‰, and pH around 7.

2. Experimental Materials

Rhizomes of *S. canadensis* and *I. cylindrica* were collected from the study area, cut to uniform size to minimize individual variation, and cultivated at the Hangzhou Bay Wetland Ecosystem Positioning Observation Station. Glyphosate isopropylamine salt was provided by Sinochem Crop Protection Co., Ltd.

3. Experimental Design

The experiment was conducted in a greenhouse in May 2016 using a De Wit replacement design [31] with two planting patterns: (1) monoculture of each species, and (2) mixed culture at 1:1 ratio. Healthy, uniformly sized plants were transplanted into plastic pots (23 cm diameter) filled with local soil. After a 2–3 week acclimation period, initial measurements were taken (height, leaf number, tiller number, leaf length). Four glyphosate concentrations were applied using a sprayer: 0 (control), 0.6, 1.2, and 1.8 mL/L. Each treatment had 6–8 replicates. Pot positions were rotated every 3 days to minimize environmental variation. After 21 days, growth indices were remeasured and light response curves were determined using a Li-COR 6400XT portable photosynthesis system.

4. Measurement Methods

4.1 Growth Index Measurement

Before and after glyphosate treatment, we measured: (1) plant height (CGh, cm) and cumulative height growth (CG = Gt - G0, where Gt is final height and G0 is initial height); (2) numbers of green, yellow, and withered leaves; (3) leaf withering rate (%) = (withered leaf length / total leaf length) × 100%; (4) tiller number; and (5) tiller mortality rate (%) = (dead tillers / total tillers) × 100%.

4.2 Light Response Curve Measurement

On clear days between 7:30-11:30, fully expanded leaves at the same position were selected and light response curves measured under ambient CO_2 (390$±20$\mu mol/mol).Photosyntheticphotonfluxdensity(PAR)wassetsequentiallyto1500,1200,1000,800,600,$ $m^{\{-2\}\cdot s}${-1}$ using red-blue light. After 240 s stabilization at each level, net photosynthetic rate (Pn, $mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (Gs, $mol \cdot m^{-2} \cdot s^{-1}$), transpiration rate (Tr, $mmol \cdot m^{-2} \cdot s^{-1}$), and intercellular CO_2 concentration (Ci, mol/mol) were recorded. Light response curves were fitted using the non-rectangular hyperbola model [33] to calculate maximum net photosynthetic rate (Pmax), light saturation point (LSP), light compensation point (LCP), apparent quantum yield (AQY), and dark respiration rate (Rd).

4.3 Data Processing and Statistical Analysis

Two-way ANOVA analyzed effects of glyphosate concentration, planting pattern, and their interaction on growth and photosynthetic parameters. When significant differences were detected ($P < 0.05$), one-way ANOVA with LSD multiple comparisons was performed. Independent t-tests compared monoculture vs. mixed culture for each species. Analyses were conducted in SPSS 19.0; figures were prepared using SigmaPlot 12.5 and Excel 2013.

5. Results

5.1 Growth Characteristics

Glyphosate significantly affected growth in both species ($P < 0.05$). Cumulative height growth of *S. canadensis* decreased with concentration, while leaf withering increased. In monoculture, height growth was 26.24%, 14.84%, 0.65%, and -14.97% of control at 0.6, 1.2, and 1.8 mL/L, respectively. Mixed-culture *S. canadensis* showed better growth (46.03%, 16.82% of control at 0.6 and 1.2 mL/L) with lower leaf withering rates, though differences between planting patterns were not significant. At 1.8 mL/L, *S. canadensis* was severely damaged with >50% leaf withering.

Imperata cylindrica was more sensitive. At 0.6 mL/L, plants turned yellow; at 1.2 mL/L, tiller mortality and leaf withering exceeded 50%; at 1.8 mL/L, mortality surpassed 70%. Mixed-culture *I. cylindrica* showed lower tiller mortality and leaf withering than monoculture, but differences were not significant. Interspecific relationship significantly suppressed *I. cylindrica* tiller number ($P < 0.05$) but not leaf length. The interaction between planting pattern and glyphosate was not significant for either species .

5.2 Photosynthetic Light Response Curves

Photosynthetic rate (Pn) increased with PAR then saturated in both species. With rising glyphosate concentration, Pn of both monoculture and mixed-culture plants declined, with *I. cylindrica* showing more rapid reduction.

Stomatal conductance (Gs) and transpiration rate (Tr) decreased with concentration. At 0.6 mL/L, monoculture *S. canadensis* Gs still increased with PAR, but mixed-culture Gs showed little response, indicating severe stomatal damage. At 1.2-1.8 mL/L, both species lost stomatal regulation capacity. Mixed-culture *S. canadensis* had higher Gs than monoculture, while mixed-culture *I. cylindrica* showed lower Gs reduction [FIGURE:3, FIGURE:4].

Intercellular CO_2 concentration (Ci) responses differed: monoculture *S. canadensis* Ci first decreased then increased with concentration, while mixed-culture Ci continuously declined. Both monoculture and mixed-culture *I. cylindrica* Ci increased with glyphosate concentration.

5.3 Photosynthetic Characteristic Parameters

Glyphosate significantly affected Pmax in both species ($P < 0.05$). In monoculture, *S. canadensis* Pmax decreased to 81.37%, 33.40%, and 21.49% of control at 0.6, 1.2, and 1.8 mL/L, respectively; mixed-culture Pmax decreased to 36.74%, 8.34%, and 4.31%. Monoculture *I. cylindrica* Pmax decreased to 24.61%, 9.24%, and 4.89%; mixed-culture decreased to 37.65% and 4.31% at 0.6 and 1.2 mL/L. Planting pattern significantly affected Pn in both species and Rd and AQY in *I. cylindrica* ($P < 0.05$).

LSP declined while LCP increased with glyphosate concentration in both species. Glyphosate did not significantly affect Rd in either species or AQY in *S. canadensis*, but significantly impacted *I. cylindrica* AQY. At 0.6 mL/L, effects on mixed-culture plants were greater than on monoculture plants. Interspecific relationship and glyphosate interaction did not significantly affect LSP, LCP, or Rd .

6. Discussion

Herbicides cause plant death by inhibiting key enzymes in secondary metabolic pathways [24]. Glyphosate, a systemic herbicide, translocates through xylem and phloem to meristematic tissues, causing chlorosis and withering within 7-10 days [6]. Our results demonstrate that native *I. cylindrica* is more sensitive to glyphosate than invasive *S. canadensis*. At low concentrations, *I. cylindrica* showed earlier chlorosis and greater damage. Compared to monoculture, mixed-culture plants of both species exhibited better growth, possibly because glyphosate reduced interspecific competition intensity and altered allelopathic root exudates from the invasive species [37-40].

Successful invaders often possess superior photosynthetic capacity [41]. *Solidago canadensis* had higher Pn and growth rates than *I. cylindrica*, facilitating its invasion. However, glyphosate significantly reduced photosynthesis in both species. The differential Ci responses indicate distinct limitation mechanisms: monoculture *S. canadensis* showed initial stomatal limitation (decreased Ci) at low concentrations, transitioning to non-stomatal limitation (increased Ci) at high concentrations as mesophyll cells were damaged. Mixed-culture *S.*

canadensis showed continuous Ci decline, indicating persistent stomatal limitation. Both monoculture and mixed-culture *I. cylindrica* exhibited increased Ci, suggesting non-stomatal limitation dominated, likely due to direct chloroplast damage [48-49].

The 0.6 mL/L concentration had greater impact on mixed-culture than monoculture plants, indicating that interspecific interactions modulate herbicide sensitivity. *Imperata cylindrica*' s greater sensitivity suggests that glyphosate application in mixed stands may disproportionately harm native species. Management recommendations should consider minimizing herbicide use when *S. canadensis* co-occurs with native species like *I. cylindrica* to reduce non-target impacts. Future research should further evaluate ecological consequences of herbicide application in invaded communities.

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Note: Figure translations are in progress. See original paper for figures.